

The disturbance regime of an Early Holocene swamp forest in the Czech Republic, as revealed by dendroecological, pollen and macrofossil data



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ABSTRACT

A unique remnant of forest dating back to the period 9733–7897 yr BC and consisting of hundreds of tree bases was discovered in the Czech Republic. We aimed to reveal the complex disturbance history of this (sub)fossil forest using dendrochronology, and to describe its detailed plant species composition changes using palaeobotanical techniques. Analysing such Early Holocene forest dynamics should help us understand the ability of the forest community to actively adapt to climate change and generally to understand the role of dynamic instability in ecosystem evolution.

We anatomically identified woody species in 488 samples, and determined the ages, growth suppressions, releases and fire scars in 116 well preserved tree ring series using a modern boundary line approach. This image of the forest structure and dynamics was supplemented with analyses of pollen spectra and plant macrofossils in excavated profiles. In order to achieve accurate dating, we dated 87 samples using ¹⁴C and synchronized tree ring series, and compared them with an existing *Pinus sylvestris* chronology.

The developmental trajectory of the forest was unique, and did not match the general trend of postglacial pine growth in central Europe. Palaeobotanical proxies indicated that during the circa 2000 years the forest persisted, this Early-Holocene ecosystem passed through several phases, reflected in the species composition of the vegetation as well as in habitat conditions. Nevertheless, the dominance of pine and the complex fine-scale disturbance regime were relatively robust and did not change fundamentally. Low-severity fires and short-term changes in soil moisture regime were crucial disturbance agents in the ecosystem. Stand-replacing disturbances were not found up to the gradual collapse of the forest around 8300 yr BC, replaced by a swamp community. The disturbance regime was relatively stable, suggesting a mitigating effect of changing climate due to the predominance of pine in the forest.

1. Introduction

Terrestrial ecosystems in the current temperate and boreal zones underwent fundamental changes during the transition from the Pleistocene to the Holocene. Rapid climate warming and humidification (e.g. Mauri et al., 2015) were accompanied by alterations in site conditions (e.g. acidification, Korhola and Tikkanen, 1991) as well as by

rapid changes in plant communities. These changing plant communities were disturbed by many factors (Johnson and Miyanishi, 2007) and were simultaneously active players in the changing disturbance regimes (Bobek et al., under review). Such dynamic ecosystem instability and the role of feedbacks between abiotic and biotic components of the ecosystems, including the role of self-organization, have been currently under intense investigation (Corenblit et al., 2011; Phillips et al., 2017).

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Pollen and plant macrofossils records have been widely used to study the regional and local development of plant community compositions since the Early Holocene (e.g. Latałowa and van der Knaap, 2006). Charcoal fragments in investigated profiles additionally allow studies of the fire disturbance history (e.g. Adámek et al., 2015; Feurdean et al., 2017). However, the character of fire footprints as well as uncertainty in dating and spatial location naturally limits detailed research on complex disturbance history. Compared to such palaeobotanical data, dendrochronological records provide more complete and readable sources of information in disturbance research, due to the complex record of events in tree radial growth and their exact dating through the synchronization of tree ring series (Friedrich et al., 2004). A detailed exploration of a disturbance regime including fire events, gap openings, and growth suppressions (flooding or drought) requires tens or even hundreds of tree ring series from a site (Šamonil et al., 2015) and additional analysis using sophisticated methodology (e.g. Frelich, 2002; Black and Abrams, 2003). Due to these demanding requirements, disturbance research has so far focused primarily on recent forest ecosystems (e.g. Panayotov et al., 2015). Analysis of the complex disturbance history of Early Holocene forest ecosystems has been lacking. The rare existing palaeo-dendrochronological studies of disturbance history (Late Glacial, Boeren et al., 2005; Mid Holocene, Leuschner et al., 2002, 2007; Edvardsson et al., 2014) unfortunately missed the critical Early Holocene period of ecosystem transformation and were solely focused on only one disturbance factor.

A unique remnant of an Early Holocene forest including hundreds of tree trunks was discovered in the central Czech Republic in late 1990s. Here, we aimed to reveal the complex disturbance history of this (sub) fossil forest using dendrochronology, and to describe temporal changes in plant species composition using wood anatomy, pollen and plant macrofossils analyses. Detailing the structure, dynamics and disturbance regime of such a forest ecosystem under past climate change should provide a realistic picture of the resilience of plant communities at that time. We also hope our research may be a source of information for predicting the evolution of the climate change framework currently under way (Thom et al., 2017).

2. Methods

2.1. Study site

The studied peat bog is located in the Czech Republic, approximately 40 km northwest of Prague (50°8'15.716"N, 13°56'33.793"E, Fig. 1). The village of Rynholec neighbours the peat bog, and we hereafter call the studied site Rynholec (Fig. 1). The site occurs at an altitude 450 m a.s.l. on unconsolidated Quaternary sediments (www.geology.cz). Current mean annual temperature is about 6.9 °C and mean annual precipitation is circa 545 mm (www.chmi.cz). Besides a small nameless stream that flows directly through the site, there are several sulphurous springs on which the peat bog developed. The high content of sulphur in the water makes the predominating Histosols (WRB, 2014) extremely acidic, with pH about 3.0, and simultaneously has allowed the relatively good preservation of Early Holocene organic materials including tree trunks.

Industrial peat mining had been practiced for a few decades on the site and ended in the late 1990s. In the extracted peat bog area, hundreds of bases of originally standing or uprooting tree trunks were uncovered. Exploratory radiocarbon dating surprisingly revealed the age of the sampled stems to be around 9000 years BC, and led to a detailed study of the development of the site (all uncalibrated dates in the text are in “yr B.P.” and all calibrated dates are in “yr B.C.”).

2.2. Data collection

Hulík (2008) positioned 273 exposed tree bases using a total station. His detailed map was completed in 2011 with newly discovered trees

(revealed as a result of the slow mineralization of the artificially drained peat). We used Field-Map technology (www.field-map.cz) during these additional measurements, resulting in a map of trees including 300 labelled tree bases (Fig. 2). In addition, there were some remnants of trees that had been moved by a dozer to a sediment mound in the 1990s. These trunk bases were sampled but not positioned in the map. In total 488 wood samples from exposed trees were collected and analysed in the laboratory to determine wood taxa.

Dendrochronological data collection was focused on all usable tree bases. In 2011 we sampled 116 trunks in total; the remaining bases were too decomposed for that purpose. First, lying trunks and the bases of standing trees were cut by a chain saw. The straight cutting surface was subsequently dried with an electric hot-air gun and the dry surface was covered by a synthetic resin. Compact solid samples were cut off the next day and packed samples were transported to the dendrochronological lab, where samples were completely exsiccated, covered by resin on the other side and then prepared for tree ring analysis. In addition, sections of the trunks were dated using ¹⁴C in the Nuclear Physics Institute of the Czech Academy of Science, Prague (www.ujf.cas.cz, see Section 2.3.2).

A standard pollen record was obtained to assess the general vegetation development of the investigated site. Field sampling was performed using a modified piston corer, 5 cm in diameter, as described by Wright Jr (1991) at an undisturbed peat profile as close as possible to the area of dead trees (Figs. 1–3). To determine the age of pollen spectra, the activity of ¹⁴C was measured in 4 samples of plant macro-remains in the Poznań Radiocarbon Laboratory (www.radiocarbon.pl) using the AMS technique.

In addition to this standard pollen record, 3 pollen spectra were sampled in peat immediately underlying 3 fallen tree trunks, whose lower surfaces, with bark still well preserved, were apparently positioned in situ. Such pollen spectra can reasonably be expected to give a pollen signal of the local vegetation. Dating of these 3 independent pollen records was considered as being at the time of tree fall, since they should have been fixed in time by the tree fall events.

To reconstruct the local vegetation succession in detail, we analysed plant macrofossil remnants in a one-meter-deep peat profile taken close to remnants of trunks (Figs. 1, 4). To determine the age of the peat sediment, 4 samples of plant macro-remains were collected and analysed in the Poznań Radiocarbon Laboratory to determine ¹⁴C age using the AMS technique.

2.3. Data processing

2.3.1. Identification of wood taxa

The collection of 488 wood samples from exposed tree bases and trunks was carried out according to a detailed map of trees (Hulík, 2008) in 2008. The samples were identified using a reflected-light microscope (Nikon Eclipse 80i) with 200–500× magnification, using standard identification keys (Schweingruber, 1990; Heiss, 2000).

2.3.2. Radiocarbon dating of tree trunks

Radiocarbon dating was used as an independent dating technique. In total 79 samples of wood, charcoal and bark were dated using ¹⁴C in the Nuclear Physics Institute of the Czech Academy of Science. Of this total, 63 tree ring samples were dated using the AMS technique (Walker, 2005, 1–3 tree rings per sample) and 16 samples (including a higher amount of C appropriate for dating, e.g. bark) by the cheaper conventional dating technique. We applied stratified random sampling, removing the shortest ring series from the selection. In 27 exceptionally long ring series we dated two samples per series as far as possible from each other. The wiggle matching technique (Bronk Ramsey et al., 2001; Galimberti et al., 2004) was applied to decrease the error of radiocarbon dating. In order to get more information about the cause and time of the forest decline, we further dated 9 bark samples and 1 burned wood sample by conventional dating. Calibration of all radiocarbon

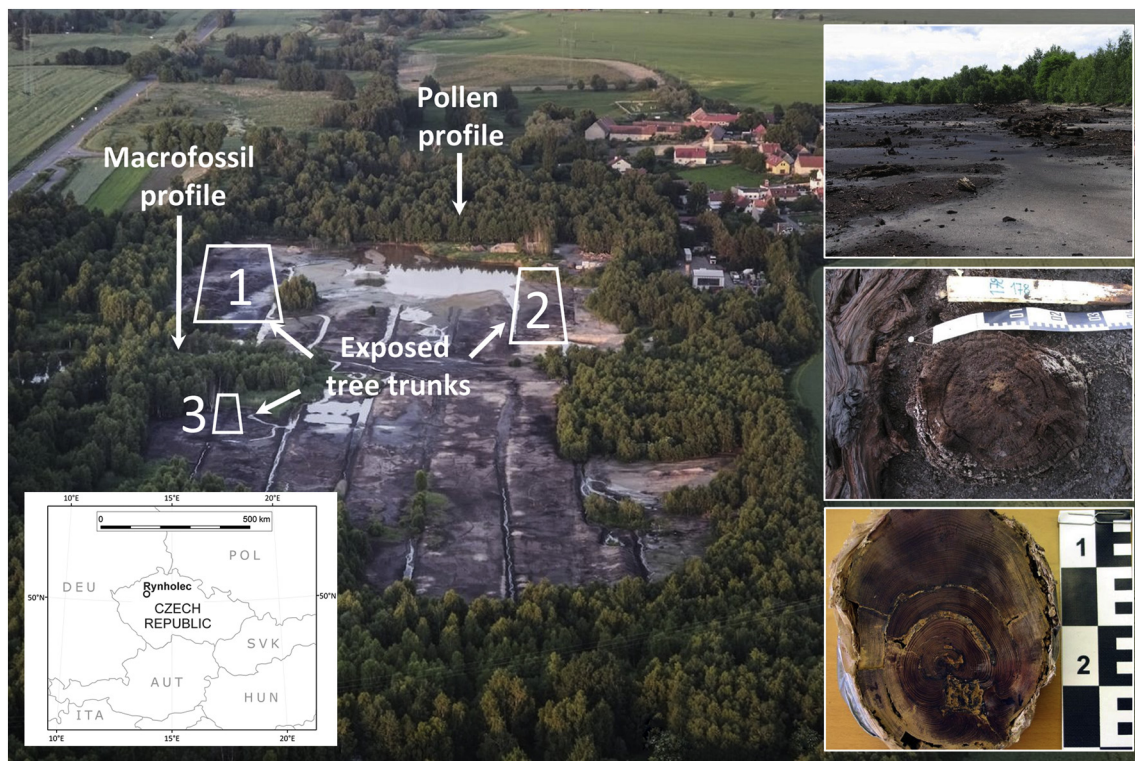


Fig. 1. Locations of exposed tree trunks, pollen and plant macrofossil profiles within the Ryhnolec peatbog. Small figures show examples of the inner structure of old-growth forest (top), exposed trunk base (middle), and trunk section (bottom) ready for dendrochronological analysis (three fire scars may be seen in the tree ring record).

data (including pollen and macrofossil profiles) via the IntCal13 curve (Reimer, 2013), determination of median ^{14}C ages, and testing of statistical differences between ^{14}C ages were done using OxCal 4.3 software (Bronk Ramsey and Lee, 2013). Testing of the differences between ^{14}C ages using the Chi-square test was used to calculate the minimal frequencies of disturbance events according to the approach by Bobek et al. (under review).

2.3.3. Dendrochronology – master chronology and disturbance history

Before the tree-ring analysis, the resin was removed from one side of the discs and the surface was smoothed with coarse, fine and very fine (400 grain) sandpaper. The surfaces of the cross-sections were prepared by cutting with surgical and razor blades and chalk powder was applied to fill the cell lumina and thus highlight the visibility of the tree-ring boundaries (Schweingruber, 1988; Cook and Kairiukstis, 1989). Tree-rings widths were measured in the direction from the pith to the bark with an accuracy of 0.01 mm using a VIAS Time Table connected to an Arsenal SZP 1100ZOOM stereomicroscope and PAST 4 software (SCIEM, 2007). At least two radii were measured for each sample to identify wedging or missing rings and possible measuring errors (see Schweingruber et al., 1990). Subsequently, the averaged tree-ring series per tree were mutually cross-matched against each other to compile the chronologies. Two statistical tests were applied to evaluate the similarities between the series. A percentage of parallel agreement, *Gleichläufigkeit*, (G), over 60 and a Student's *t*-test over 3.5 were considered to be sufficient and significant. Finally, statistically cross-matched series were visually inspected to confirm the reliability of the compiled chronologies. We then asked colleagues from Hohenheim University, Germany, to compare our floating master chronologies (particularly our longest chronology including 12 synchronized tree ring series, see Section 3) with existing deep and robust chronologies published by Becker and Kromer (1993), Friedrich et al. (2004), Kaiser et al. (2012), and Schaub et al. (2008). Chronologies were compared in terms of the parallel agreement and Student's *t*-test in PAST 4 and a place of

agreement was sought (see Friedrich et al., 2004).

To obtain a comprehensive picture of forest dynamics including the disturbance regime, scars and growth changes in the tree-ring series were evaluated. We used the standard anatomical features of individual events (Schweingruber, 1996, 2007) and the knowledge of natural conditions at the site to interpret these features. The cambium is disturbed when a tree is damaged (mechanically or by heat) and the tree naturally makes an effort to close the injury by increasing the activity of the adjacent cambium. This results in a typical structure in the radial tree growth record called a “scar”, a commonly analysed feature in many dendrochronological studies (Schweingruber, 1990). Because micro-charcoal fragments were found in some scars, these were interpreted to be footprints of fire events (see Lagueard et al., 2000). Moreover, micro- and macro-charcoal fragments were very common in the sediment (see plant macrofossil and pollen profiles descriptions below). Positive and negative growth changes, i.e. growth releases and suppressions, were evaluated based on precisely measured widths of tree rings by standard dendrochronological procedures (see Šamonil et al., 2013).

To identify releases in radial growth we first calculated a boundary line (BL) according to Black and Abrams (2003). This approach, established in modern forest ecosystem studies, helps identify growth responses to disturbances in relation to preceding growth rate. As far as we know, however, this approach has not yet been used in palaeo-dendrochronological analyses. In the first step, the level of potential growth response in relation to the prior growth is determined; i.e. a boundary line function is calculated. Then, the individual growth changes are compared with the level of the BL and disturbance pulses are determined.

Detailed calculation of the BL requires the detection of prior growth and growth change for each tree ring of all tree ring series (Nowacki and Abrams, 1997). For prior growth we used the absolute mean annual increment of the 10 yr preceding any annual ring, and for growth change the percent change of mean annual increment between two 10-

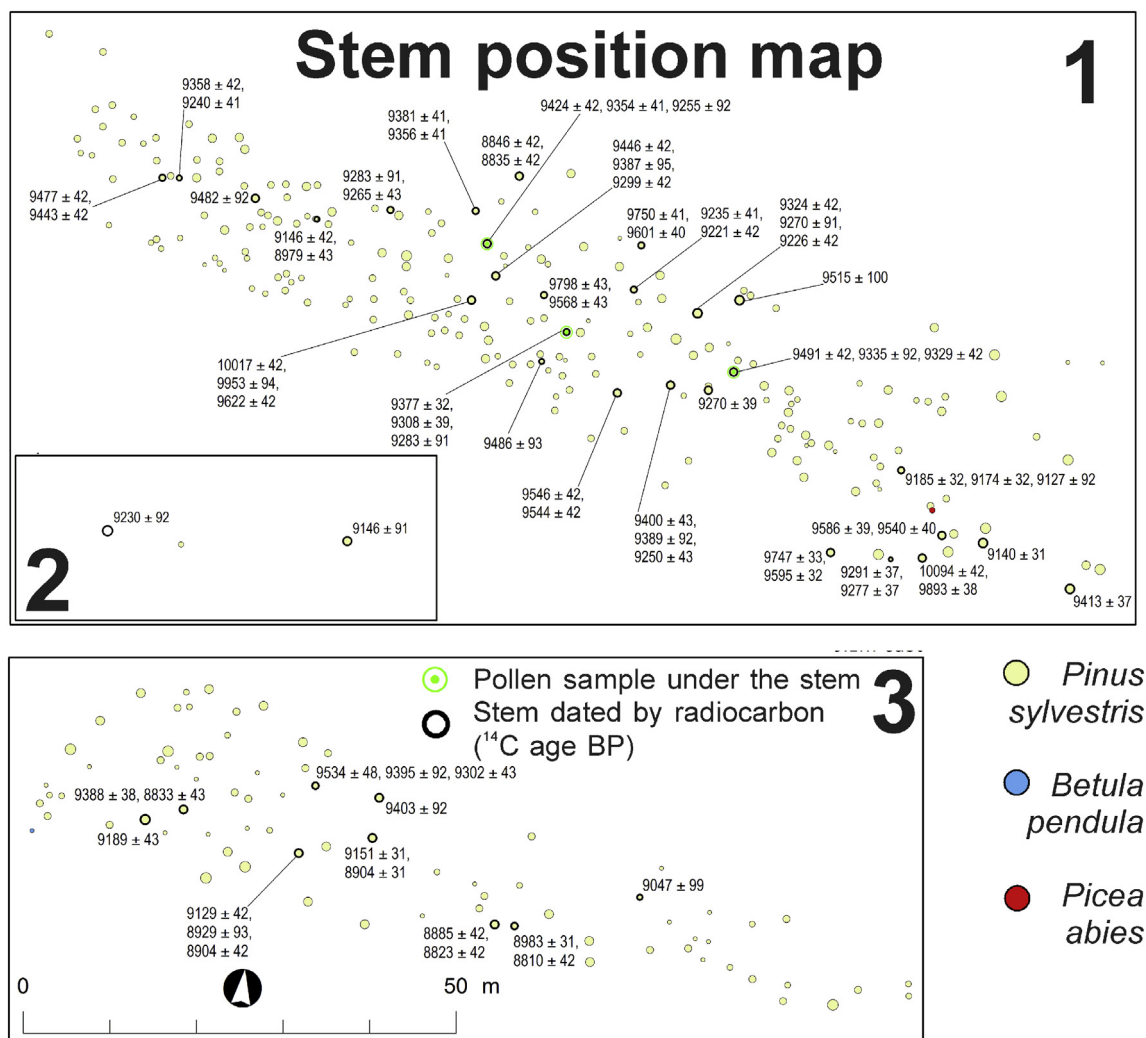


Fig. 2. Stem position map with positions of pollen samples taken under the trees. The size of a mark represents the diameter of the tree trunk at the surface; trunks dated by ^{14}C are emphasized.

yr intervals. We subsequently divided the whole set of 13,090 prior growths of *Pinus* spp. into 0.5 mm wide intervals. Because of high values of growth changes, intervals up to 1 mm of prior growth were divided into shorter intervals of 0.25 mm, according to [Splechna et al. \(2005\)](#) and [Šamonil et al. \(2013\)](#). The 10 highest values (or 5 in the case of the shorter 0.25 intervals) were subsequently fitted by an exponential curve constructed using the Nonlinear Least Squares function in R ([R Core Team, 2017](#)) using the TRADER package ([Altman et al., 2014](#)), and the BL function was determined. Although [Black et al. \(2009\)](#) recommended circa 50,000 growth impulses as minimal in northern hardwoods in the USA, much smaller data sets including only few thousands of growth increments have successfully been used in some forest ecosystem studies (e.g. [Szwagrzyk and Szweczyk, 2001](#); [Zielonka and Marcher, 2009](#)). Our approach, recommended in a comparative study by [Rubino and McCarthy \(2004\)](#), enabled us to remove false releases produced by short-term climatic changes.

The determined local growth maxima were subsequently compared with the boundary line values in order to establish which growth change maxima represented a release. Growth changes falling within 50–100% of the BL were classified as a moderate release, and changes exceeding 100% of the BL were classified as a major release ([Nowacki and Abrams, 1997](#)). Responses below 50% of the BL (including minor releases, see [Šamonil et al., 2013](#)) were disregarded as unreliable (see details regarding uncertainty in [Vašíčková et al., 2016](#)).

To identify suppressions in growth we used an analogous approach,

and a negative boundary line (NBL) was calculated. To construct the NBL we fitted the 10 (or 5) lowest values of each prior growth interval. Moderate and major suppressions were classified if reaching 50–100% BL and $> 100\%$ NBL, respectively. It should be noted that the sudden death of a tree due to an extreme event cannot be identified by dendrochronological techniques due to methodological limitations (see [Lorimer and Frelich, 1989](#); [Nowacki and Abrams, 1997](#)).

Differences in the frequencies of disturbance counts between types of disturbance (fires, suppressions, and releases) and forest developmental stage (initial, main, late) were assessed using generalized linear models (GLM) with Poisson distribution corrected for overdispersion. We used mean annual event counts for each tree-ring sequence as a response variable, group membership as an explanatory variable and tree-ring sequence lengths as weights in the GLMs. Significant differences between tree groups were identified based on pairwise p -values using a sequential Bonferroni-type procedure ([Benjamini and Hochberg, 1995](#)) with $\alpha = 0.05$. Different ^{14}C ages of trees ([Fig. 2](#)) prevented a spatial analysis of the disturbance history and relationships between tree individuals.

2.3.4. Pollen analysis – a local to regional record of vegetation composition

Pollen analyses were performed on two types of samples. First, a continuous peat core, 520 cm long, was sampled in a still-undisturbed location of the peat bog ([Figs. 1, 3](#)). This pollen record consisted of 60 individual samples, and according to radiocarbon data and their

Rynholec, 50°08'13"N, 13°57'02"E; 407 m a.s.l.

pollen percentage diagram (selected taxa only)

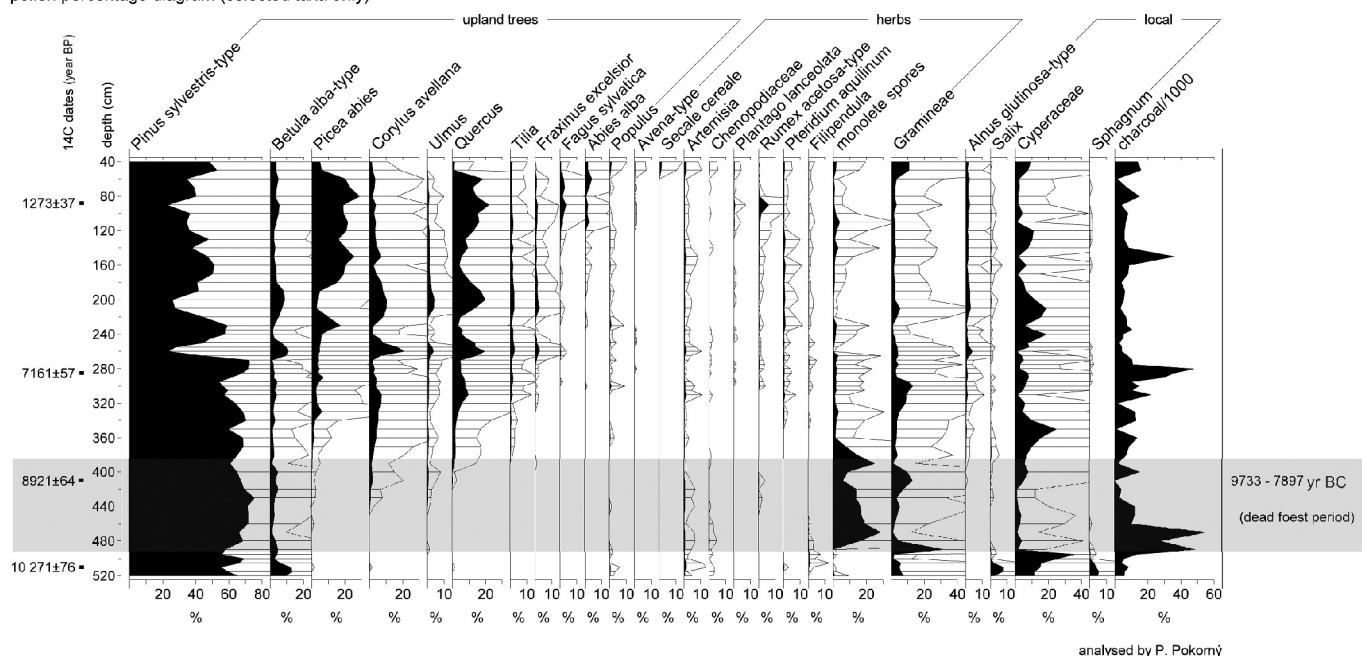


Fig. 3. Record of pollen spectra in an undisturbed peat profile near the tree trunks. For position see Fig. 1.

calibration covers about the last 12,000 years (i.e. from the YD phase of the Late Glacial to the present) without obvious hiatuses. Second, 3 individual pollen samples were taken in a peat surface buried below 3 lying pine trunks (Fig. 2); these samples allowed the reconstruction of local vegetation composition at the moment when each of the trunks fell to the ground.

All samples intended for pollen analyses were treated by a modified acetolysis method (Erdtman, 1960). As most sediment contained some mineral particles, the samples were pre-treated with concentrated (35%) cold hydrofluoric acid (HF) for 24 h (Moore et al., 1991). Extracted microfossils were stained by 0.3% safranin and mounted in a glycerol-water (1:1) mixture. In each sample at least 700 pollen grains were counted. For pollen identification a reference collection and the following keys were used: Faegri and Iversen (1989), Moore et al. (1991), and Beug (2004). Pollen nomenclature follows PALYCZ (The

Czech Palynological Data-Base; Kuneš et al., 2009). In the pollen-analytical samples, microscopic charcoal particles were calculated using the point-count method described by Tolonen (1986).

The resulting pollen percentage diagram (Fig. 3) is based on the terrestrial AP + NAP pollen sum, i.e. excluding only demonstrable aquatic taxa but including *Pteridium*, *Equisetum*, and all monolete spores (as in most plant communities these taxa usually have an ecological role equivalent to that of higher plants). Concealed, corroded, degraded, and well preserved but indeterminable pollen grains were grouped together as “varia”. The diagram was made in the Tilia computer program (Grimm, 2015), and was zoned visually on the basis of both the presence and abundance of ecologically important taxa. The microscopic charcoal curve was calculated as the ratio between the total pollen sum (AP + NAP) and the number of particles.

AMS radiocarbon dating of the pollen sequence was performed on

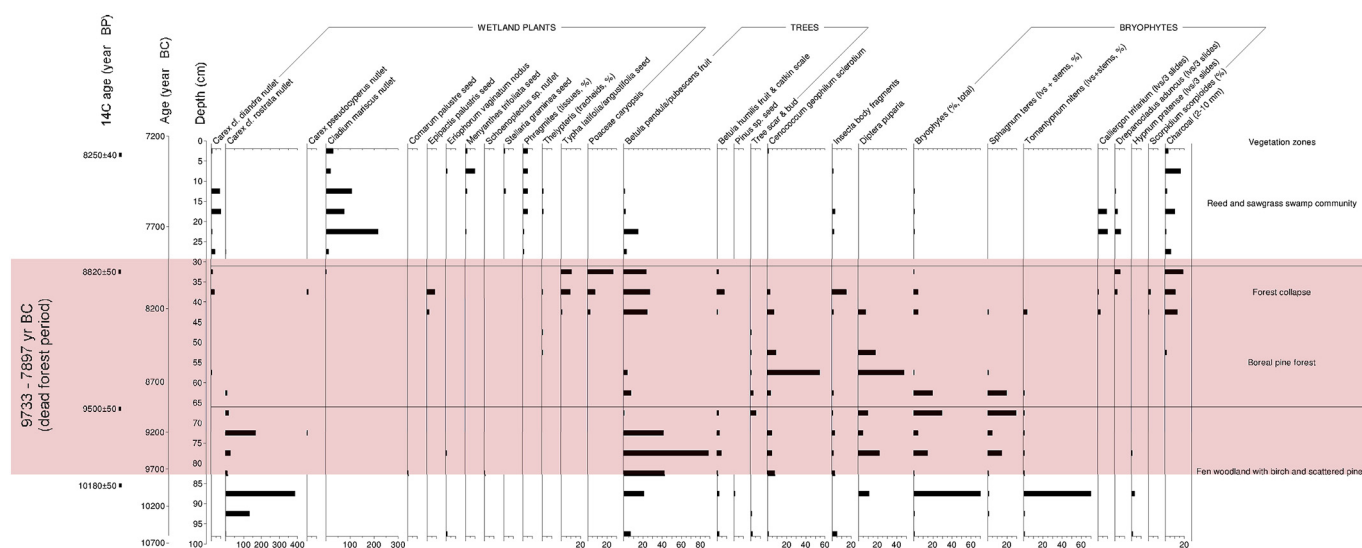


Fig. 4. Record of plant macrofossils expressed as concentrations per 50 ml. The abundance of a dominant bryophytes species was expressed as percentage distributions (%) or counts of leaves/seeds per 3 microscopic slides (1/3 s; s/3 s).

plant macrofossils at the *Physikalisches Institut der Universität Erlangen-Nürnberg*. A depth-age model was calculated by linear interpolation between the midpoints of the calibrated ranges of four available ^{14}C dates (Reimer et al., 2004). No reservoir or hardwater effects were assumed. The present surface of the deposit (0 cm) was considered to be dated as 0 yr BP (1950 CE; shortly after 1950 CE the site was drained and at the same moment the accumulation of peat probably stopped).

2.3.5. Plant macrofossil analysis - local vegetation composition

The plant macrofossil analysis was conducted in 5 cm intervals. Due to the high concentration of plant remains in the samples, 50 ml of the sediment was found to be sufficient for the analysis. This volume was measured by the displacement of water in a measuring cylinder and the sediment was washed through a 200 μm sieve (Birks, 2001). Then, the generative and vegetative parts of plant remains were determined using a dissecting microscope at a magnification of 15 \times or higher. Plant macrofossils were identified by comparison with the reference collection as well as by published keys and atlases (Katz et al., 1977; Tomlinson, 1985; Cappers et al., 2006; Bojnanský and Fargašová, 2007). The results were expressed as a concentration per defined volume and visualized in the macrofossil diagram created in Tilia v. 2.0.41 (Grimm, 2015).

The depth-age model for the macrofossil profile was based on linear interpolation between dated samples performed in the program R using the script Clam 2.2 (Blaauw and Christen, 2011), with the IntCal13 curve used for calibration of the AMS radiocarbon dates (Reimer, 2013).

3. Results

3.1. Pollen record – a local to regional record of vegetation change

According to the results of radiocarbon dating of the pollen record (Fig. 3) and interpolation between the individual radiocarbon dated levels, the depths between 420 cm and 320 cm are roughly synchronous with the time of the existence of the studied forest (see Section 3.3). This period was framed by significant micro-charcoal peaks around 9800 and 8000 yr BC, suggesting fire events. The pollen record during the studied forest phase shows an absolute dominance of pine and a gradual increase in the percentage of broadleaf species (*Corylus*, *Ulmus*, *Quercus*, *Tilia*) and spruce (*Picea*) in the tree layer of the regional vegetation cover. Some non-forest vegetation still persisted from the previous (Late Glacial) period, as shown above all by the *Artemisia* curve. As for the local development of the wetland, *Cyperaceae*, willow (*Salix*), grasses (*Gramineae*) and ferns (see the Monoletes spores category in the pollen diagram – Fig. 3) alternate. This alternation can be interpreted as a reflection of some hydrological or trophic changes at the site. Although such an interpretation of local vegetation changes is somewhat vague, it is clear that the development of local vegetation as revealed by the pollen diagram was highly dynamic.

The three pollen spectra from under the trunks (Table 1) can be to some extent correlated with the main pollen profile, and thus confirm their ^{14}C age. Under two trunks (nos. 122 and 137) we found grass-dominated pollen spectra. In addition, these samples contain many microscopic charcoal particles. These characteristics indicate that they probably came from a relatively dry local vegetation phase with the occurrence of fires. Under the third trunk (designation X14), on the contrary, pollen grains of grasses and microscopic charcoal particles are relatively rare. This pollen spectrum is strongly dominated by *Betula*, which indicates that birch was abundant in the local canopy. The fact that birch trunks are almost absent from the megafossil record (see below) can be interpreted by their immediate or later (post-depositional) decomposition.

Table 1

Record of pollen spectra under three lying tree trunks. For position see Fig. 2.

Pollen spectra under lying tree trunks	Trunk No. 122	Trunk No. 137	Trunk No. X14
<i>Anthemis t.</i>	2	3	2
<i>Apium repens t.</i>		1	
<i>Artemisia</i>	10	6	2
<i>Aster t.</i>		1	
<i>Asteraceae Subfam. Liguliflorae</i>			1
<i>Betula alba t.</i>	404	364	2220
<i>Calluna vulgaris</i>		3	
<i>Caltha t.</i>			2
<i>Corylus</i>	24	26	8
<i>Cruciferae</i>	1		
<i>Cyperaceae</i>	10	13	25
<i>Equisetum</i> (spores)	4	3	1
<i>Filipendula</i>	13	18	4
<i>Gelasinospora</i> (ascospores)			1
<i>Gramineae</i> (under 50 μm)	592	526	97
<i>Gramineae</i> (above 50 μm)			1
<i>Heracleum</i>	1		
<i>Hydrocotyle vulgaris</i>	1	1	
<i>Juniperus</i>		1	1
<i>Labiatae</i>	1	2	1
<i>Melampyrum</i>	6	2	
<i>Mentha t.</i>			1
<i>monoletes spores</i>	11	4	7
<i>Picea</i>	2	3	4
<i>Pinus</i>	1028	670	408
<i>Quercus</i>	6	2	2
<i>Ranunculus acris t.</i>			1
<i>Rubiaceae</i>	1	1	
<i>Salix</i>	15	21	6
<i>Sanguisorba</i>			1
<i>Sordaria</i> (ascospores)			2
<i>Sphagnum</i> (spores)	9	20	4
<i>Thalictrum</i>	2		2
<i>Tilletia sphagni</i> (spores)	2	33	1
Charcoal (above 10 μm)	13,608	248,832	1335
<i>Ulmus</i>	16	12	9
<i>Umbelliferae</i>	14	5	3
VARIA	4	3	2
<i>Vicia t.</i>		3	

3.2. Plant macrofossil record - local vegetation composition

The plant macrofossil record (Fig. 4) covers the period between 10,700–7300 yr BC. A fen woodland with birch and scattered pines appeared at the site from ca 10,700 to ca 8900 yr BC; we interpret this period as an initial forest phase. Accumulation of peat deposits at Rynholec started during the Younger Dryas/Holocene transition around 10,700 yr BC. During this period a mire community became established, and a few hundred years later birches and several pines arrived. The mire community was characterised by wetland plants (*Carex rostrata*, *Carex vesicaria*, *Comarum palustre*, *Eriophorum* sp.) and bryophytes (*Tomentypnum nitens*, *Hypnum pratense*, *Sphagnum teres*). Around 10,000 yr BC, a pioneer birch forest, consisting of downy birches (*Betula pubescens*) as well as shrubby birches (*Betula humilis*), started to predominate over the fen species. The predominance of this birch forest was accompanied by an observable decline in light-demanding and wet-loving species such as *Carex rostrata* and *Tomentypnum nitens*.

A mire pine woodland occurred at the site from ca 8900 to ca 8300 yr BC, reflecting the main forest phase. As the mire pine woodland expanded, the local vegetation went through substantial changes. Most of the wetland species disappeared and the peat soil started to dry out. Many wood fragments as well as other tree indicators were preserved in the sediment (leaf scars, buds). Importantly 70% (19/27) of the dated pine megafossils correspond to this period, again documenting the expansion of forest at the locality throughout this period. In addition, sclerotia of the ubiquitous ectomycorrhizal fungi *Cenococcum geophilum* were found, while other plant macrofossils were almost completely

absent. The occurrence of *Cenococcum geophilum* points to relatively dry soil conditions during this period.

The forest gradually collapsed from circa 8300 to circa 7900 yr BC; indicating a phase of forest decline. Around 8300 yr BC the mire pine forest started to die out and nutrient rich fen vegetation became re-established. The local vegetation community was represented by the wetland plants *Carex diandra*, *Epipactis palustris*, *Typha latifolia*, as well as the bryophytes *Scorpidium scorpioides* and *Calliergon trifarium*. The tree *Betula pubescens* and shrub *Betula humilis* became dominant in the canopy (likely very sparse), as evidenced by frequent findings of birch fruits and catkin scales. In addition, the percentage of radiocarbon dated pine megafossils fell below 25%, indicating a gradual retreat of the pine forest (6/27). An increasing amount of macro charcoal > 2 mm compared to the previous phase suggests more common fires (Fig. 4).

After circa 7900 year BC, a reed and sawgrass swamp community developed at the site, initiating a swamp phase. Even though findings of birch fruits and catkin scales indicating a few scattered birches were still present at the site, no evidence of a local occurrence of birch was recorded after 7400 yr BC. Similarly, no pine megafossils were preserved from that time period. The swamp sawgrass (*Cladium mariscus*), a light-demanding species and strong competitor, became dominant. The swamp sawgrass community was accompanied by *Phragmites* sp., *Carex diandra* and *Menyanthes trifoliata* taxa with a preference for relatively higher mineral levels. The amount of charcoal was comparable with the phase of forest decline.

3.3. Dendrochronology – woody species composition and the radiocarbon age of tree trunks

Extensive radiocarbon dating of 79 woody samples found median forest ^{14}C ages ranging from 9733 to 7897 yr BC (see the raw data in Fig. 5). Thus the trunks at the site represent circa 2000 years of the development of the forest ecosystem, which began immediately at transition between the last Weichselian (Würmian) glaciation, i.e. the Younger Dryas (11,000–9500 BC), and the warmer Pre-Boreal

(9000–8200 BC) and then Boreal (8200–7000 BC) periods of the Holocene (for stratigraphy see e.g. Bos, 2001, Walanus and Nalepka, 2010). *Pinus sylvestris* clearly predominated in this record, with 483 woody samples positively identified. *Picea/Larix* type was identified in 4 cases, indicating the existence of a glacial refugium in the region. Only one tree trunk was identified as *Betula* sp., in contrast to the frequent presence of *Betula* in the macrofossil record (the species-specific decomposition of trunks is the most likely explanation).

About one half of the exposed trees came from the main phase of mire forest development as identified by the plant macrofossil record (Section 3.2). A quarter of tree individuals were from the initial phase of forest development and the remaining quarter from the period of forest decline after 8300 yr BC.

3.4. Plasticity of tree growth and chronology

The tree ring series expressed enormous plasticity even at the level of individual trees. More than 20% of the series originating from the same tree trunk did not reach $G = 60$. This threshold was required as a crucial criterion in the synchronization of tree ring series between individual trees (see Section 2). The variability understandably increased when tree-ring series were compared between tree individuals, and only a few ring series achieved the strict similarity criteria for synchronization. We successfully synchronized the tree-ring series of 12 trees in the main phase of forest growth (19 ^{14}C dates included, the length of the chronology reaches almost 300 years) and an additional 4 tree ring series in the initial phase of postglacial forest establishment (one ^{14}C date included). Two additional floating chronologies including 6 and 4 tree individuals, respectively, originated from the youngest phase of forest decline (2 and 3 radiocarbon ages, respectively, were included).

The dendrochronological record did not generally reflect the formerly published overall trends in growth driven by climate in the Early Holocene, and likely rather reflected specific local conditions. Comparison of our floating chronologies with an existing unique 12,460-year Hohenheim oak and pine tree ring chronology from

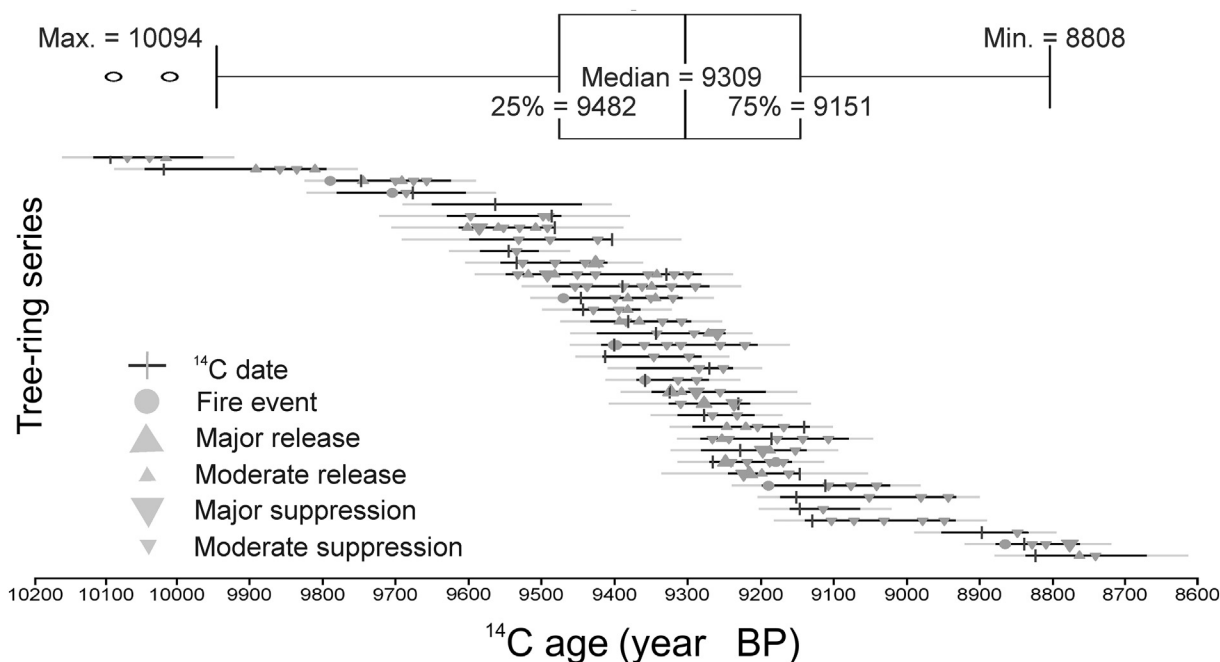


Fig. 5. Distribution of tree-ring series dated by radiocarbon and the main characteristics of their distribution (raw uncalibrated data are given). Box plots show statistics of the ^{14}C dates. While Q1 roughly corresponds with the initial phase of forest development, Q2 and Q3 correspond to the main phase of mire forest and Q4 to the phase of forest decline. Grey circles or triangles represent different types of disturbance events, while grey lines on the edges of tree-ring series represent uncertainty in series positions from ^{14}C dating.

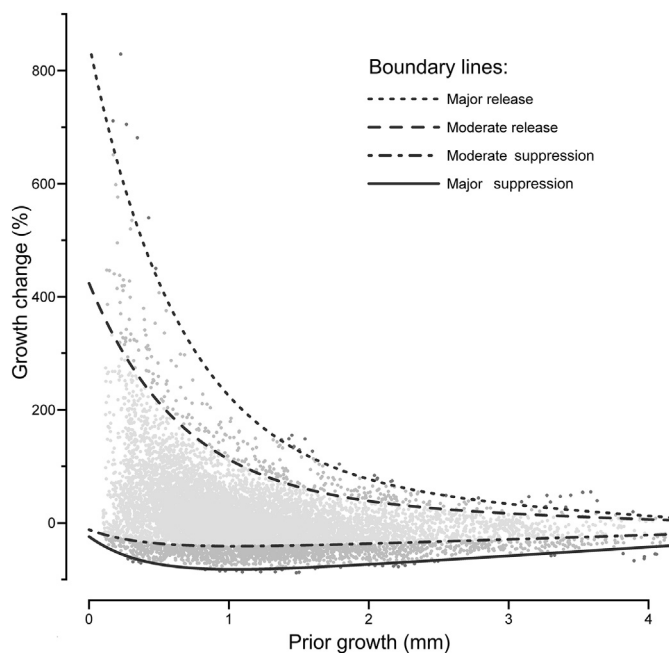


Fig. 6. Potential growth plasticity of *Pinus* spp. at the site. The point cloud represents growth changes in relation to prior growth in 13,090 growth increments in the data set. Positive and negative boundary lines and the curves of 50% of BLs, determining major and moderate disturbance events, are shown.

Central Europe (Friedrich et al., 2004) did not result in any matches. This indicates that our floating chronologies were not entirely accurately dated. However, individual synchronized or non-synchronized tree ring series dated by radiocarbon completely occupied 2 thousand years of forest development (Fig. 5), most of them belonging to the main phase of forest growth. Uncertainties of ^{14}C dates were in some cases significantly decreased by wiggle matching to a minimum of 38 years (Figs. 2, 5), and a three-century-long chronology was established between 8746 and 8708 yr BC.

In total, 13,090 growth increments were recorded from 116 tree growth series, with a maximal tree age of 267 years. The potential response of trees to release is expressed by a positive boundary line (BL), whereas the potential response of trees to deteriorated growth conditions is expressed by a negative BL (Fig. 6). The positive boundary line had the function $70.522 - 14.962x + 777.006 * \exp(-1.525x)$, and the negative BL had the function $-105.031 + 15.589x + 80.898 * \exp(-2.408x)$. An increase of negative BL values with increasing prior growth in the zone of rapid growth suggests a gradual rather than abrupt response of trees to disturbances.

The potential response of pines to disturbance events was the highest during the main forest phase (circa 8300–8900 yrs BCE), and hence a partially positive boundary line was moved up compared to the initial forest phase or forest decline. However, this partial boundary line lay at the edge of the 95% confidence interval of the general BL, and we therefore consider the growth plasticity to be generally uniform over the studied 2000 years.

3.5. Disturbance regime of the forest

Fire scars, growth suppressions and releases were evaluated over circa 2000 years of recorded forest history (Table 2, Figs. 2, 5, 7, Appendix 1). In total 15 scars were determined, particularly in the juvenile tree growth stage, representing circa 0.23 fire events per 100 years of the growth record. Furthermore, 251 total positive or negative responses to disturbances were found in the entire dendrochronological record. Suppressions were significantly more frequent than releases. The appearance of major suppressions almost reached the

frequency of fire scars (0.2 suppressions per 100 years of record), while major releases were rare (only 0.1 releases per 100 years). Moderate suppressions and releases were understandably more frequent than the major events (but these events are at the same time burdened by a greater uncertainty of detection, see Vašíčková et al., 2016). Our dendrochronological results suggest that the forest dynamics were primarily driven by fire and changing moisture regimes, documented by the local vegetation assemblage at the site, and secondarily by releases in growth. The disturbance regime visible in the tree ring series was relatively robust throughout the whole forest duration. Neither the frequencies of major releases, types of suppressions, or fires differed statistically among the phases of forest development (Table 2). Only the frequency of moderate releases significantly decreased from the initial to the main and finally to the late phase of forest development. We did not find significant synchronicity in the occurrence of scars, suppressions, or releases in tree ring chronologies.

The extensive radiocarbon dating of trees (Figs. 5, 7) allowed us to calculate the minimal frequencies of disturbance events over the entire 2000-year studied period. We found evidence for four independent fire events, three major suppressions, two major releases and numerous moderate suppressions and releases (Fig. 8). The occurrences of moderate suppressions and sometimes also moderate releases were more frequent than the widths of the confidence intervals of individual radiocarbon dates (Figs. 5, 7). In such cases we determined the crucial periods of moderate suppressions and releases rather than their individual frequencies. The actual frequencies of these events were most likely significantly higher. This conclusion is supported by the analysis of 300 years in the main forest phase, where synchronization of the tree-ring series was successful (Fig. 9).

The circa 300 year-long chronology of synchronized trees uncovered a detailed partial disturbance history of the forest (Fig. 9). We found four fire scars belonging to two separate fire events with a recurrence time of circa 140 years. As mentioned above, growth suppressions (46 moderate and 4 major suppressions) were more common than releases. We found only 14 moderate and 1 major release in the longest chronology. In extreme decades, 50–70% of trees expressed suppression, most probably due to flood events. This suggests that the recurrence time of such periods of suppressed growth was 30–50 years.

4. Discussion

4.1. Growth plasticity of trees and growth chronology

The unique data analysed in this study enhance the picture of postglacial succession of terrestrial ecosystems in Central Europe that has been established from regional case studies from various periods of the Holocene (e.g. Pilcher et al., 1995; Gunnarson, 2001; Moir et al., 2010). A majority of existing chronologies of pine (Eronen et al., 1999; Eckstein et al., 2009) and oak (Pilcher et al., 1984; Jansma, 1996; Leuschner et al., 2000, 2002) cover solely the younger Holocene and do not go back to its earliest phase, the period of Last Glacial ecosystem rebuilding under the influence of rapid climate warming (e.g. Borzenkova et al., 2015). Or, vice versa, some individual chronologies record the older Late Glacial period but do not extend to the earliest Holocene (e.g. Friedrich et al., 1999, 2001, 2003; Kaiser et al., 2012). These two critical periods, the Late Glacial and Early Holocene, have only been connected in the Hohenheim pine and oak tree-ring chronology (Becker and Kromer, 1993; Spurk et al., 1998; Friedrich et al., 2004), providing a unique continual and general dendrochronological record of the developmental trajectory of forest ecosystems. At Rynholec, environmental conditions as well as the observed trajectory of ecosystem development showed significant deviations to that general trend (e.g. Friedrich et al., 2004). We therefore consider this study to be a unique example of a postglacial ecosystem succession. Analysing such specific developmental trajectories may help us understand the validity of general ecological rules in the succession of terrestrial ecosystems

Table 2

Record of disturbances in relation to time period. Small letters (a–b) indicate differences between time periods – if two values share a common letter, there is not a significant difference between them and vice versa.

Period	Variable	Fire scars	Moderate growth suppressions (50–100% BL)	Major growth suppressions ($\geq 100\%$ BL)	Moderate growth releases (50–100% BL)	Major growth releases ($\geq 100\%$ BL)
The whole period	Sum of indications	15	191	11	42	7
	Relative frequency of indications per tree	0.20	2.58	0.15	0.57	0.09
	Mean per 100 years	0.22 ^a	3.02 ^a	0.20 ^a	0.72 ^b	0.11 ^a
Initial phase of forest development	Sum of indications	2	20	2	13	0
	Relative frequency of indications per tree	0.25	2.5	0.25	1.63	0
	Mean per 100 years	0.15 ^a	1.54 ^a	0.19 ^a	1.06 ^b	0
Main phase of forest development	Sum of indications	7	106	11	28	5
	Relative frequency of indications per tree	0.23	3.53	0.37	0.93	0.17
	Mean per 100 years	0.15 ^a	2.00 ^a	0.21 ^a	0.50 ^{ab}	0.13 ^a
Late phase of forest development	Sum of indications	3	41	2	5	1
	Relative frequency of indications per tree	0.21	2.93	0.14	0.36	0.07
	Mean per 100 years	0.16 ^a	1.86 ^a	0.13 ^a	0.22 ^a	0.05 ^a

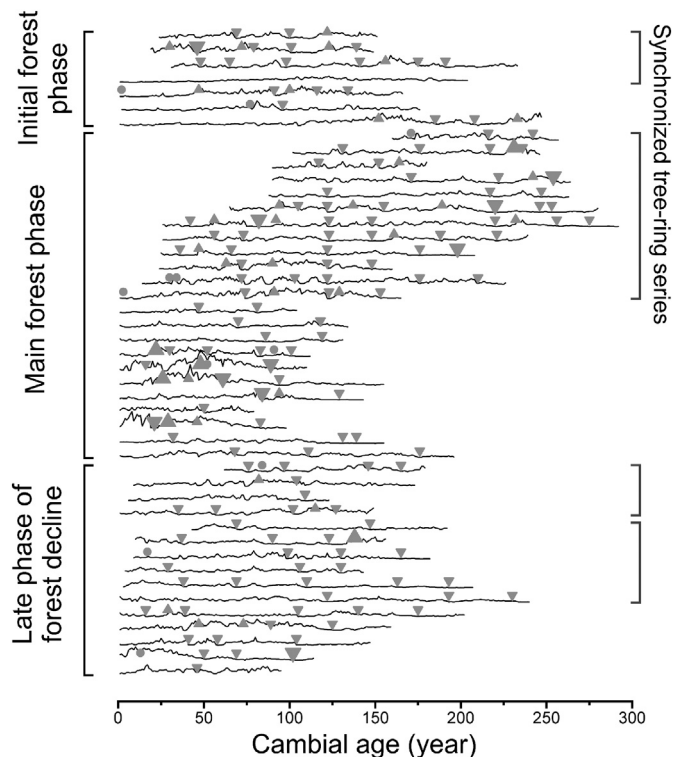


Fig. 7. Annual growth of *Pinus sylvestris* dated by radiocarbon in the initial, main and late phases of forest development; grey circle – fire events, grey large triangle on top – major suppression, grey small triangle on top – moderate suppression, grey large triangle on base – major release, grey small triangle on base – moderate release. Successfully synchronized tree-ring series are in brackets. For methodological details see Section 2.

(see the effect of historical contingency in Phillips, 2013).

The low replicability of our tree-ring series resulted in a lower robustness of the results compared to central European reference chronologies (Friedrich et al., 2001; Leuschner et al., 2002). The failure to synchronize our floating chronology with existing chronologies reaching the Early Holocene (Becker and Kromer, 1993; Spurk et al., 1998; Friedrich et al., 2004) may be due to local specifics of pine growth on peat bogs in the region. The mire community was characterised by wetland plants (*Carex rostrata*, *Carex vesicaria*, *Comarum palustre*, *Eriophorum* sp.) and bryophytes (*Tomentypnum nitens*, *Hypnum*

pratense, *Sphagnum teres*) that indicate minerotrophic groundwater-fed wetlands, i.e. fens (Hájek et al., 2006, see also Eckstein et al., 2011). Our results correspond with those of Cedro and Lamentowicz (2011), who found that pines growing on a peat bog showed no clear relationship with meteorological conditions, while the typical response of pine to climate was visible only on terrestrial soils. Soil temperature and moisture also drove the radial growth of *Pinus sylvestris* in Central Yakutia, Russia (Nikolaev et al., 2009), though this was associated with the permafrost dynamics at that site.

The low replicability of our tree-ring series even within the site reflects enormous local growth plasticity, probably due to local differences in the depth of the water table and the generally swampy character of the site. Other authors have also described difficulties in the synchronization of *Pinus sylvestris*, for example Friedrich et al. (2004) suggested a high tendency for missing rings in this species. However, core-series from higher-elevation peat bogs saturated primarily by precipitation and not by groundwater have sometimes been successfully synchronized (Eckstein et al., 2009).

We did not observe a replacement of *Pinus sylvestris* by *Quercus* spp. as described for example by Friedrich et al. (2004) in a synthetic European study. On the contrary, our pollen record suggested a long-term predominance of *Pinus sylvestris* at the site throughout the entire Holocene. This may be due to local environmental conditions, particularly the acidic soils that tend to become waterlogged. A similar local long-term dominance of *Pinus sylvestris* caused by an extremely nutrient-poor quartz-rich and sandy soil was described in the Czech Republic by Novák et al. (2012). These results suggest the significance of local site conditions in the post-glacial colonization by woody species and the formation of specific plant communities.

The occurrence of *Picea abies* trunks at the site with a median radiocarbon age of 8041 yr BCE (8897 ± 98 yr BP) is evidence of the relatively early expansion of spruce in the region. Spruce macrofossils of the same age (median cal ^{14}C age = 8029 BC, i.e. 8874 ± 80 yrs. BP) were found in the Novohradske Mts. in the southern Czech Republic (Bobek et al., under review). Latałowa and van der Knaap (2006) also suggested that *Picea abies* expanded rigorously even during the Allerød, contracted or stagnated during the Younger Dryas, and then strongly re-expanded during the Preboreal in Central Europe (see also Willis and van Andel, 2004). They used pollen data, which generally have substantial uncertainty regarding the local occurrence in comparison to plant macrofossils. These occurrences preceded the large colonization of central Europe by spruce. An extensive DNA and pollen analysis by Tollefsrud et al. (2008) concluded that the entire Czech lands were rapidly colonized by spruce before 8000 yr BP.

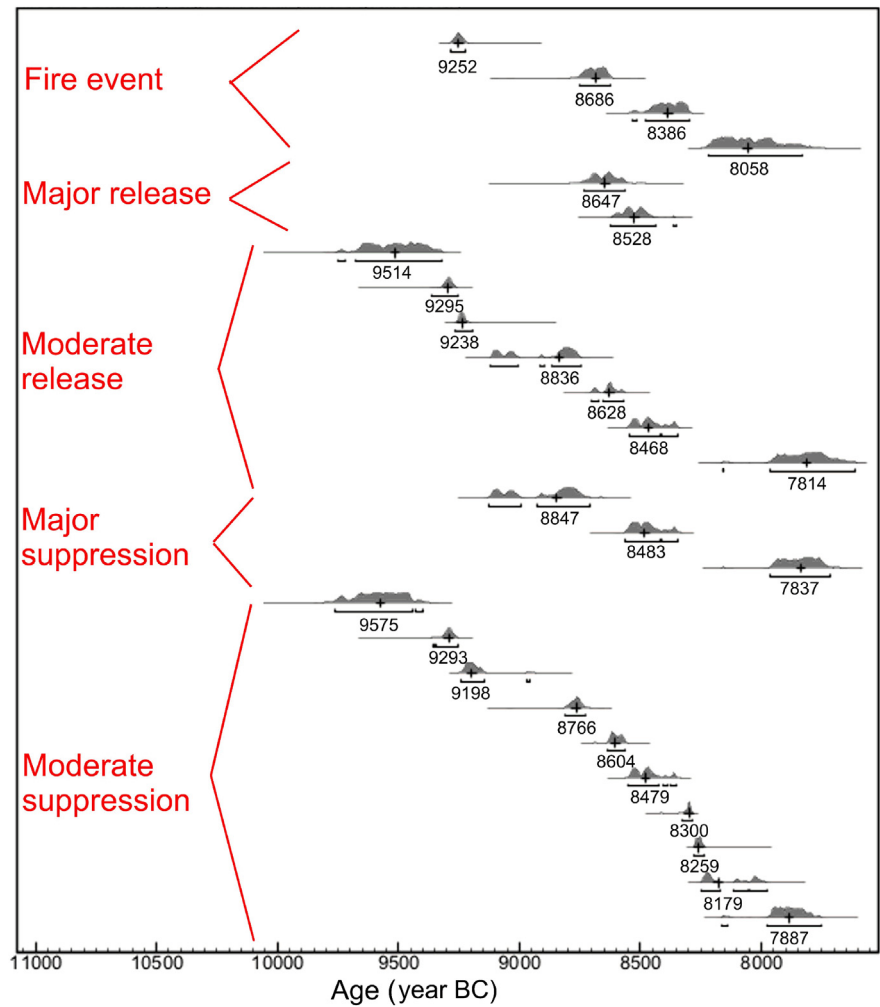


Fig. 8. Significantly differing groups of disturbance events calculated as merged probability distributions of radiocarbon dates (see Fig. 5). Statistical significance was tested by a pairwise Chi-square test in OxCal 4.3.

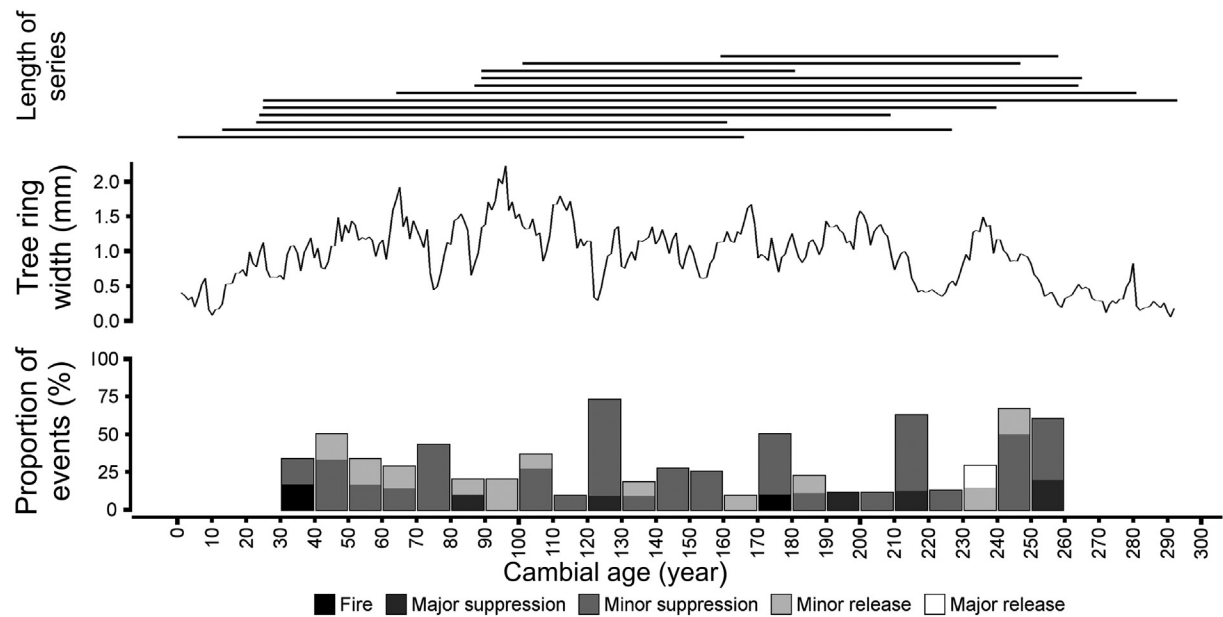


Fig. 9. The approximately 300-year-long period of main phase of forest development covered by the best replicated curve build from 12 trees. The overlay of individual tree-ring series as well as synchronized main chronology are shown. The histogram represents canopy disturbed area; the relative proportion of disturbance events is shown only for periods when the amount of samples is higher than four.

4.2. Disturbance history and forest collapse

In contrast to former studies focused solely on analyses of fire scars and historical fire disturbance regimes (e.g. [Lageard et al., 2000](#)), we were able to associate fire disturbances with clearly determined releases and suppressions in the radial growth of trees. While a scar represents unambiguous evidence of a disturbance event, growth changes are always indirect indications of disturbances. Growth responses may be not only powerful, abrupt and long-term, but also weak, gradual, or short-term ([Lorimer and Frelich, 1989](#)). Connecting growth changes to a disturbance history requires a sensitive approach because arbitrary decisions during data processing may significantly affect the obtained results ([Rubino and McCarthy, 2004](#)). Identifying disturbance events based on growth changes may technically limit the analysis of the whole disturbance history. We employed a dendrochronological approach used in modern old-growth temperate forests (e.g. [Splechtna et al., 2005](#); [Šamonil et al., 2013](#)), where sample size is not generally as limited and mathematical accuracy is critically required (e.g. [Frelich, 2002](#)). Low sample sizes have made analyses of disturbance history in many palaeo-dendrochronological studies impossible (e.g. [Moir, 2012](#), see the evaluation of uncertainty by [Šamonil et al., 2015, 2016](#)). We believe that some innovations used here regarding disturbance history calculations are also applicable in other palaeo-dendrochronological studies analysing at least tens of tree-ring series.

As far as we know, the boundary line approach established by [Black and Abrams \(2003\)](#), and used as a credible technique in current old-growth forests (e.g. [Splechtna et al., 2005](#); [Black et al., 2009](#); [Zielonka et al., 2010](#); [Szewczyk et al., 2011](#); [Šamonil et al., 2013](#); [Vašíčková et al., 2016](#)), has not yet been used on palaeo-dendrochronological data (e.g. [Moir, 2012](#)), probably due to general limits in the amount of available increment cores in very old dendrochronological material (but see comparable paleo-data sets by e.g. [Edvardsson et al., 2015](#)). [Black et al. \(2009\)](#) recommended circa 50,000 annual rings for evaluating tree growth plasticity. No boundary line has yet been built in forests dominated by *Pinus sylvestris*, and only few have been built in forests dominated by different species within the genus *Pinus* (*P. ponderosa*, *P. echinata*, *P. strobus* in [Black et al., 2009](#), *P. palustris* in [Bhuta et al., 2008](#)). Our study is also the first to calculate a negative boundary line. At the same time, the novelty of our approach makes the comparability of results regarding growth plasticity of trees more difficult. As expected, the ability of *Pinus sylvestris* to react to release under still relatively cold and dry climate at the beginning of the Holocene at Rynholec was usually smaller than the responses of trees in current forest ecosystems. For instance, the boundary line at Rynholec did not reach the values of BLs calculated for current *Pinus echinata* ([Black et al., 2009](#)) or *Pinus palustris* ([Bhuta et al., 2008](#)) forests in the US, current Central-European old-growth mountain beech ([Splechtna et al., 2005](#); [Vašíčková et al., 2016](#)) or spruce ([Zielonka et al., 2010](#)) forests, or for North American forests dominated by *Tsuga canadensis* ([Black et al., 2009](#)). On the other hand, the potential responses of *Pinus sylvestris* in our study usually exceeded the responses of *Quercus stellata* in the US ([Black et al., 2009](#)) and *Larix decidua* in the Tatra Mts., Slovakia ([Zielonka et al., 2010](#)). As at our site, those stands are exposed to strong climatic stress (drought, short growth season etc.). Of course, the amount of analysed data affects the resulting BL ([Vašíčková et al., 2016](#)) and this may complicate the comparability of BLs.

The algorithmic approach of disturbance detection used at Rynholec revealed a complex disturbance regime for the pine forest. Because of the Palaeolithic age of the forest, we assume natural rather than artificial origins of the disturbance events (e.g. [Smiljanić et al., 2014](#)). Anthropogenic plant indicators in the pollen record such as *Avena* sp. and *Plantago lanceolata* were absent in the studied period ([Fig. 3](#)). The high local variability of disturbances may have decreased the potential of tree ring series to be replicated. Our low number of synchronized tree ring series, and therefore construction of only short chronologies consisting of maximally 12 tree-ring series, is in good accordance with the

complex fine scale disturbance regime of the forest. The enormous local plasticity of the dendrochronological record was probably a reflection of the fundamental significance of microsite conditions in the radial growth of trees, particularly due to the variable position of the water table in relation to microphotography (see [Cedro and Lamentowicz, 2011](#)). The synchronization of suppressions with charcoal remains in Raichwalde, Germany ([Friedrich et al., 2003](#)) suggesting a changing water table due to the effect of fire was not clearly seen in our data. We observed rather an independent impact of fine scale disturbance factors. However, the occurrence of wetland or even aquatic plant species after some charcoal peaks in the pollen and macrofossil records may suggest the existence of this synchronicity at Rynholec as well.

Surprisingly, fire frequencies at Rynholec were significantly lower compared to Late Glacial or some analogous recent or subfossil forests dominated by *Pinus sylvestris*. For example, according to [Boeren et al. \(2005\)](#) the dynamics of Late-Glacial pine forests in Germany were fundamentally driven by fire regime. [Ivanova et al. \(2010\)](#) found the interval between fire events to be only about 10–20 years in Tuva (Russia), and [Niklasson and Drakenberg \(2001\)](#) found a recurrent fire interval of about 20 years in the Middle Ages in southeastern hemiboreal *Pinus sylvestris* forests in Sweden. [Niklasson and Drakenberg \(2001\)](#) concluded that such a frequency was 4 times higher than in pine forests in northern Sweden. Northern Swedish forests also expressed relatively low fire severity ([Niklasson and Granstrom, 2000](#)), which is another similarity with our palaeo-record from Rynholec. The low fire severity at Rynholec is demonstrated by the low proportion of trees with fire scars and by their occurrence in usually juvenile aged trees (with thin bark). We speculate that at our site the low frequency and severity of fires resulted in the non-significant growth changes after fires as well as the minor impacts to the moisture regime (see above). In contrast to [Lageard et al. \(2000\)](#), who observed a rejuvenating effect on *Pinus sylvestris* woodlands expressed by increasing tree ring widths after a fire event, we found no such dependence in our data.

Significant positive growth changes were generally assumed to be growth releases due to canopy opening (e.g. [Lorimer and Frelich, 1989](#)). Inversely, significant negative growth changes were most likely due to waterlogging at the site (e.g. [Leuschner et al., 2002](#)). This interpretation corresponds well with the concave topography of site, the proximity of the stream, the occurrence of hygrophilous plant species in macro fossil and pollen records ([Figs. 3 and 4](#)), the joint response of many trees in the population ([Figs. 9](#)) as well as the soil properties driven particularly by water (with gleyic and histic soil horizons predominating, see [WRB, 2014](#)). Our interpretation of positive growth changes through gap opening is supported by the very local occurrence as well as the often short distances between trees of the same age ([Fig. 2](#)). However, the impacts of other factors such as extreme frost events ([Camarero et al., 2015](#)), or biotic factors ([Linares et al., 2014](#)) cannot be excluded.

The extensive random dating of trees revealed a gradual decrease in dated individuals as forest dieback proceeded, suggesting a gradual rather than abrupt forest collapse. We assume that the increasing water table was accompanied by a decreasing number of trees at the site. This is supported by the plant macrofossil record, which indicates a gradual transition from a mire pine forest to reed swamp vegetation. Trees may have actively supported this process. Tree roots may reduce the moisture content of surface peat layers through evapotranspiration ([Boggie, 1972](#)), and retreating trees together with local burning, documented by macro-charcoal fragments and fire scars, could have potentially accelerated the process of waterlogging that led to the establishment of the reed swamp vegetation. A similar process, which could be characterised as paludification ([Schaffhauser et al., 2016](#)), and which is recently typical in the boreal biome, was also described by [Moir et al. \(2010\)](#) in Scotland. On the contrary, [Mighall et al. \(2004\)](#) described a rapid dieback of *Pinus sylvestris* in Ireland c 4000 yr BP along with increased mire surface wetness as a result of a change in climate.

Age structure is an important component of forest dynamics. In their Late-Glacial study from Germany, Friedrich et al. (2003) found 87% of trees younger than 110 years and only some tree individuals reaching 150 years. In our study, the average age of trees was 138 years, with 13% of trees older than 200 years, and a maximal age of 267 years. Moreover, it should be noted that for some of the trees in our study this is a minimum age, because the series were not always complete due to the surface decomposition of trunks. A higher average age may be related to the decrease in fire frequency and generally by the reduced extreme growth conditions at the onset of the Holocene. This supports our assumption that fine scale disturbances predominated in the Early-Holocene forest dynamics at our site.

5. Conclusions

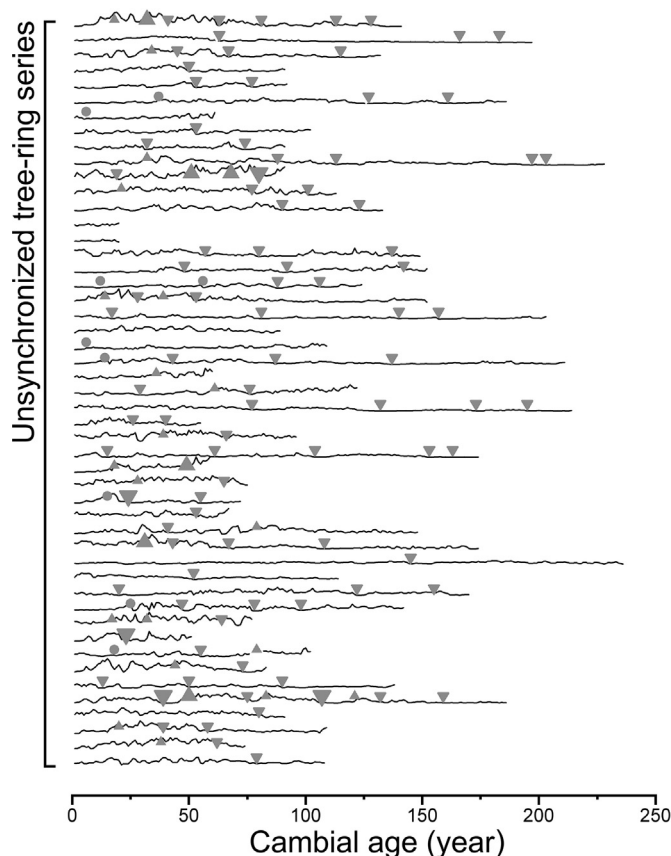
The Early Holocene forest at the Rynholec peat bog developed differently from the general record from published central European pine chronologies. *Pinus sylvestris*, which dominated at the site throughout the Holocene, was accompanied by *Picea abies* and *Betula* spp. soon after the Late Glacial, suggesting the existence of glacial refugia in the region. A complex fine-scale disturbance regime consisting of infrequent low-severity fires, short-term changes in the moisture regime and occasional canopy opening resulted in an enormous local plasticity of tree

radial growth. The site experienced no stand-replacing events over 2000 years until the gradual collapse of the forest community around 7900 yr BC to a swamp community. Although the forest underwent changes over those two thousand years in the herb layer and habitat characteristics (indicated by identified plant remains), the dominance of pine and the associated disturbance regime seems to have been robust and did not change significantly. This suggests that the predominance of a single tree species, specifically *Pinus sylvestris*, may decrease the effects of changing climate.

Acknowledgments

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Appendix 1. Annual growth of *Pinus sylvestris* not dated by radiocarbon in the initial, main and late phases of forest development; grey circle – fire events, grey large triangle on top – major suppression, grey small triangle on top – moderate suppression, grey large triangle on base – major release, grey small triangle on base – moderate release. For methodological details see [Section 2](#)



Appendix 2. List of radiocarbon dates used for pollen, macrofossil and dendrochronological analyses, $p = 95.4\%$ (in order to simplify and shorten the table, partial age intervals have been linked in expression of calibrated age)

Lab. ID	Character of data	Type of dated material	Sample depth	^{14}C age	Uncertainty	Calibrated age
			(cm)	(year BP)	(\pm year)	(year BC/AD)
Poz-56242	Macrofossil profile	<i>Cladium mariscus</i> nutlets, <i>Menyanthes trifoliata</i> seeds	3–4	8250	40	7454–7091
Poz-56241		<i>Betula</i> sp. seeds & catkin scales, <i>Menyanthes trifoliata</i> seeds, <i>Pinus/Picea</i> seed	32–33	8820	50	8206–7737
Poz-56243	Pollen profile	<i>Carex</i> cf. <i>vesicaria</i> nutlets, <i>Betula</i> sp. seeds	66–67	9500	50	9131–8640
Poz-56305		moss stems, <i>Carex</i> sp. seeds	85–86	10,180	50	10,126–9679
Erl-4511		unidentified twig	88	1273	37	661–865 AD
Erl-4626		<i>Carex</i> sp., stem	285	7161	57	6209–5912
Erl-4513		unidentified twig	410	8921	64	8276–7839
Erl-4514		unidentified twig	510	10,271	76	10,441–9811
15_069	Dedrochronological samples	Tree rings		10,094	42	10,009–9453
15_057		Tree rings		10,017	42	9795–9360
11209		Tree rings		9953	94	9851–9255
15_070		Tree rings		9893	38	9443–9276
15_048		Tree rings		9798	43	9319–9220
15_411		Tree rings		9750	41	9294–9160
15_401		Tree rings		9747	33	9286–9189
15_058		Tree rings		9622	42	9225–8828
15_410		Tree rings		9601	40	9193–8813
15_402		Tree rings		9595	32	9176–8817
15_408		Tree rings		9586	39	9176–8801
15_047		Tree rings		9568	43	9155–8780
15_061		Tree rings		9546	42	9140–8760
15_062		Tree rings		9544	42	9140–8758
15_407		Tree rings		9540	40	9137–8755
15_391		Tree rings		9534	48	9141–8745
8254		Tree rings		9515	100	9221–8621
15_067		Tree rings		9491	42	9121–8643
11202		Bark		9486	93	9180–8571
11205		Tree rings		9482	92	9176–8569
15_049		Tree rings		9477	42	9119–8634
15_059		Tree rings		9446	42	9108–8619
15_050		Tree rings		9443	42	9107–8617
15_065		Tree rings		9424	42	8812–8606
15_382		Tree rings		9413	37	8792–8612
11206		Tree rings		9403	92	9130–8351
15_043		Tree rings		9400	43	8780–8569
11196		Bark		9395	92	9124–8349
11207		Tree rings		9389	92	9121–8347
15_051		Tree rings		9388	38	8759–8566
11200		Bark		9387	95	9121–8345
15_055		Tree rings		9381	41	8761–8558
15_405		Tree rings		9377	32	8742–8567
15_053		Tree rings		9358	42	8750–8489
15_056		Tree rings		9356	41	8747–8489
15_066		Tree rings		9354	41	8746–8488
11194		Bark		9335	92	8821–8301
15_068		Tree rings		9329	42	8720–8463
15_045		Tree rings		9324	42	8718–8456
15_406		Tree rings		9309	39	8704–8355
15_390		Tree rings		9302	43	8702–8351
15_060		Tree rings		9299	42	8700–8349
15_072		Tree rings		9291	37	8636–8351
11197		Bark		9283	91	8738–8299
11199		Bark		9283	91	8738–8299
15_071		Tree rings		9277	37	8625–8349
11208		Tree rings		9270	91	8724–8296

15_409	Tree rings	9270	39	8621–8347
15_388	Tree rings	9265	43	8620–8340
11198	Bark	9255	92	8712–8289
15_044	Tree rings	9250	43	8606–8325
15_054	Tree rings	9240	41	8594–8313
15_063	Tree rings	9235	41	8567–8311
11204	Tree rings	9230	92	8702–8281
15_046	Tree rings	9226	42	8560–8307
15_064	Tree rings	9221	42	8556–8306
15_383	Tree rings	9189	43	8542–8295
15_400	Tree rings	9185	32	8533–8297
15_399	Tree rings	9174	32	8527–8293
15_403	Tree rings	9151	31	8453–8287
11203	Tree rings	9146	91	8614–8231
15_387	Tree rings	9146	42	8527–8278
15_398	Tree rings	9140	31	8451–8281
15_394	Tree rings	9129	42	8462–8269
11193	Bark	9127	92	8622–8021
8255	Tree rings	9047	99	8551–7946
15_397	Tree rings	8983	31	8284–7991
15_386	Tree rings	8979	43	8286–7977
11195	Bark	8929	93	8291–7757
15_395	Tree rings	8904	42	8245–7946
15_404	Tree rings	8904	31	8227–7965
8256	Tree rings	8897	98	8284–7734
15_393	Tree rings	8885	42	8235–7843
15_385	Tree rings	8846	42	8208–7793
15_384	Tree rings	8835	42	8206–7756
15_052	Tree rings	8833	43	8205–7756
15_392	Tree rings	8823	42	8203–7748
15_396	Tree rings	8810	42	8199–7733
8257	Charcoal	8808	98	8223–7615

References

- Adámek, M., Bobek, P., Hadincová, V., Wild, J., Kopecký, M., 2015. Forest fires within a temperate landscape: a decadal and millennial perspective from a sandstone region in Central Europe. *For. Ecol. Manag.* 336, 81–90.
- Altman, J., Fibich, P., Dolezal, J., Aakala, T., 2014. TRADER: a package for tree ring analysis of disturbance events in R. *Dendrochronologia* 32, 107–112.
- Becker, B., Kromer, B., 1993. The continental tree-ring record – absolute chronology, C-14 calibration and climatic-change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 103, 67–71.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* 57, 289–300.
- Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München.
- Bhuta, Bhuta A.R., Kennedy, L.M., Copenheave, C.A., Sheridan, P.M., Campbell, J.B., 2008. Boundary-line growth patterns to determine disturbance history of remnant longleafpine (*Pinus palustris* P. Mill.) in mixed forests of Southeastern Virginia. *J. Torrey Bot. Soc.* 135, 516–529.
- Birks, H.H., 2001. Plant macrofossils. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic Publishers, Dordrecht, pp. 49–74.
- Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal.* 6, 457–474. <https://doi.org/10.1214/11-BA618>.
- Black, B.A., Abrams, M.D., 2003. Use boundary-line growth patterns as a basis for dendroecological release criteria. *Ecol. Appl.* 13, 1733–1749.
- Black, B.A., Abrams, M.D., Rentch, J.S., Gould, P.J., 2009. Properties of boundary-line release criteria in North American tree species. *Ann. For. Sci.* 66, 205–213.
- Bobek, P., Šamonil, P., Jamrichová, E., 2018. Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *J. Quat. Sci.* (under review since April 2017).
- Boeren, I., Stika, H.-P., Knipping, M., Friedrich, M., Küppers, M., 2005. Fire and water. The dendro-ecological reconstruction of a Late-Glacial pine forest in Reichwalde, E-Germany. In: Sarlatto, Mara, Di Filippo, Alfredo, Piovesan, Gianluca, Romagnoli, Manuela (Eds.), *Abstract Book of Eurodendro 2005 - International Conference of Dendrochronology*. Publisher: Sette Città, pp. 43–44.
- Boggie, R., 1972. Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland. *Oikos* 23, 304–312.
- Bojňanský, V., Fargašová, A., 2007. Atlas of Seeds and Fruits of Central and East-European Flora. In: *The Carpathian Mountains Region*. Springer, Dordrecht.
- Borzenkova, I., Zorita, E., Borisova, O., Kalniņa, L., Kisieliene, D., Koff, T., Kuznetsov, D., Lemdahl, G., Sapelko, T., Stančikaitė, M., Subetto, D., 2015. Climate change during the Holocene (past 12,000 years). Second assessment of climate change for the Baltic Sea Basin. *Reg. Clim. Stud.* 24–49. https://doi.org/10.1007/978-3-319-16006-1_2.
- Bos, J.A.A., 2001. Lateglacial and Early Holocene vegetation history of the northern Wettetau and the Amöneburger Bain (Hessen), central-west Germany. *Rev. Palaeobot. Palynol.* 115, 177–212.
- Bronk Ramsey, C., Lee, S., 2013. Recent and planned developments of the program OxCal. *Radiocarbon* 55, 720–730.
- Bronk Ramsey, C., van der Plicht, J., Weninger, B., 2001. 'Wiggle matching' radiocarbon dates. *Radiocarbon* 43, 381–389.
- Camarero, J.J., Gazol, A., Sancho-Benages, S., Sanguesa-Barreda, G., 2015. Know your limits? Climate extremes impact the range of Scots pine in unexpected places. *Ann. Bot.* 116, 917–927.
- Cappers, R.T.J., Bekker, R.M., Jans, J.E.A., 2006. *Digitale Zadenatlas van Nederland*, Groningen Archaeological Studies. Vol. 4 Barkhuis Publishing & Groningen University Library, Groningen.
- Cedro, A., Lamentowicz, M., 2011. Contrasting responses to environmental changes by pine (*Pinus sylvestris* L.) growing on peat and mineral soil: An example from a Polish Baltic bog. *Dendrochronologia* 29, 211–217.
- Cook, E.R., Kairiukstis, L.A. (Eds.), 1989. *Methods of Dendrochronology*. Kluwer Academic Publishers, Boston.
- Corenblit, D., Baas, A.C.W., Bornette, G., Darrozes, J., Delmotte, S., Francis, R.A., Gurnell, A.M., Julien, F., Naiman, R.J., Steiger, J., 2011. Feedbacks between geomorphology and biota controlling earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Sci. Rev.* 106, 307–331.
- Eckstein, J., Leuschner, H.H., Bauerochse, A., Sass-Klaassen, U., 2009. Subfossil bog-pine horizons document climate and ecosystem changes during the Mid-Holocene. *Dendrochronologia* 27, 129–146.
- Eckstein, J., Leuschner, H.H., Bauerochse, A., 2011. Mid-Holocene pine woodland phases and mire development – significance of dendroecological data from subfossil trees from northwest Germany. *J. Veg. Sci.* 22, 781–794.
- Edvardsson, J., Poska, A., Van der Putten, N., Rundgren, M., Linderson, H., Hammarlund, D., 2014. Late-Holocene expansion of a South Swedish peatland and its impact on marginal ecosystems: evidence from dendrochronology, peat stratigraphy and palaeobotanical data. *The Holocene* 24, 466–476.
- Edvardsson, J., Rimkus, E., Corona, C., Simanauškiene, R., Kazys, J., 2015. Exploring the impact of regional climate and local hydrology on *Pinus sylvestris* L., growth variability – a comparison between pine populations on peak soils and mineral soils in Lithuania. *Plant Soil* 392, 345–356.

- Erdtman, G., 1960. The acetolysis method, a revised description. *Sven. Bot. Tidskr.* 54, 561–564.
- Eronen, M., Hyvärinen, H., Zetterberg, P., 1999. Holocene humidity changes in northern Finnish Lapland inferred from lake sediments and submerged Scots pines dated by tree-rings. *The Holocene* 9, 569–580.
- Fægri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*, IV Edition. John Wiley and Sons, Chichester.
- Feurdean, A., Florescu, G., Vannière, B., Tantău, I., O'Hara, R., Pfeiffer, M., Hutchinson, S.M., Gaika, M., Moskal-Del Hoyo, M., Hickler, T., 2017. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *For. Ecol. Manag.* 389, 15–28.
- Frelich, L.E., 2002. *Forest Dynamics and Disturbance Regimes Studies from Temperate Evergreen-deciduous Forests*. Cambridge University Press, Cambridge, New York.
- Friedrich, M., Kromer, B., Spurk, M., Hofmann, J., Kaiser, K.F., 1999. Paleo-environment and radiocarbon calibration as derived from Lateglacial/Early Holocene tree-ring chronologies. *Quat. Int.* 61, 27–39.
- Friedrich, M., Kromer, B., Kaiser, K.F., Spurk, M., Hughen, K.A., Johnsen, S.J., 2001. High-resolution climate signals in the Bølling-Allerød Interstadial (Greenland Interstadial 1) as reflected in European tree-ring chronologies compared to marine varves and ice-core records. *Quat. Sci. Rev.* 20, 1223–1232.
- Friedrich, M., Boeren, I., Remmele, S., Küppers, M., Eschenbach, C., Knipping, M., Stika, H.-P., Böttger, T., Vollbrecht, J., Renno, A., Ullrich, O., 2003. A Late-Glacial forest in the lignite mine of Reichwalde – an interdisciplinary project. In: Schleser, G., Winiger, M., Bräuning, A., Gärtner, H., Helle, G., Jansma, E., Neuwirth, B., Treyde, K. (Eds.), *TRACE – Tree Rings in Archaeology, Climatology and Ecology*, Vol. 1: Proceedings of the DENDROSYMPOSIUM 2002, April 11th - 13th 2002, Bonn/Jülich, Germany. Vol. 33. Schriften des Forschungszentrums Jülich, Reihe Umwelt, pp. 90–91.
- Friedrich, M., Remmele, S., Kromer, B., Hofmann, J., Spurk, M., Kaiser, K.F., Orzel, C., Küppers, M., 2004. The 12,460-year Hohenheim oak and pine tree ring chronology from Central Europe – a unique annual record for radiocarbon calibration and paleoenvironment reconstructions. *Radiocarbon* 46, 1111–1122.
- Galimberti, M., Bronk Ramsey, C., Manning, S.W., 2004. Wiggle-match dating of tree-ring sequences. *Radiocarbon* 46, 917–924.
- Grimm, E.C., 2015. *Tilia Software*. Illinois State Museum, Springfield.
- Gunnarson, B.E., 2001. Lake level changes indicated by dendrochronology on subfossil pine, Jamtland, central Scandinavian mountains, Sweden. *Arct. Antarct. Alp. Res.* 33, 274–281.
- Hájek, M., Horsák, M., Hájková, P., Dítě, D., 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspect. Plant Ecol. Evol. System.* 8, 97–114.
- Heiss, A.G., 2000. *Anatomy of European and North American woods - an interactive identification key*. Version 2006-08-22. Available at: <http://www.holzanatomie.at/>.
- Hulík, L., 2008. *Virtuální rekonstrukce archeologické lokality*. Bc-Thesis. Czech Technical University in Prague, Prague.
- Ivanova, G.A., Ivanov, V.A., Kukavskaya, E.A., Soja, A.J., 2010. The frequency of forest fires in Scots pine stands of Tuva, Russia. *Environ. Res. Lett.* 5, 015002.
- Jansma, E., 1996. An 1100-year tree-ring chronology of oak for the Dutch coastal region. *Tree Rings*. In: Dean, J.S., Meko, D.M., Swetnam, T.W. (Eds.), *Radiocarbon*, Department of Geology. University of Arizona, Tucson.
- Johnson, E.A., Miyaniishi, K. (Eds.), 2007. *Plant Disturbance Ecology—The Process and the Response*. Elsevier, Burlington.
- Kaiser, K.F., Friedrich, M., Miramont, C., Kromer, B., Sgier, M., Schaub, M., Boeren, I., Remmele, S., Talamo, S., Guibal, F., Sivan, O., 2012. Challenging process to make the Lateglacial tree-ring chronologies from Europe absolute – an inventory. *Quat. Sci. Rev.* 36, 78–90.
- Katz, N.J., Katz, S.V., Skobeeva, E.I., 1977. *Atlas of Plant Remains in Peat*. Nedra, Moscow.
- Korhola, A.A., Tikkanen, M.J., 1991. Holocene development and early extreme acidification in a small hilltop lake in southern Finland. *Boreas* 20, 333–356.
- Kuněš, P., Abraham, V., Kovář, O., Kopecký, M., Břízová, E., Janovská, V., Knipping, M., Kožáková, R., Nováková, K., Petr, L., Pokorný, P., Rozková, A., Rybníčková, E., Svobodová-Svitavská, H., Wacnik, A., 2009. Czech Quaternary Palynological Database – PALYCZ: review and basis statistics of the data. *Preslia* 81, 209–238.
- Lageard, J.G.A., Thomas, P.A., Chambers, F.M., 2000. Using fire scars and growth release in subfossil Scots pine to reconstruct prehistoric fires. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164, 87–99.
- Latalowa, M., van der Knaap, W.O., 2006. Late Quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. *Quat. Sci. Rev.* 25, 2780–2805.
- Leuschner, H.H., Spurk, M., Baillie, M., Jansma, E., 2000. Stand dynamics of prehistoric oak forests derived from dendrochronologically dated subfossil trunks from bogs and riverine sediments in Europe. *Andean Geol.* 11, 118–121.
- Leuschner, H.H., Sass-Klaassen, U., Jansma, E., Baillie, M.G.L., Spurk, M., 2002. Subfossil European bog oaks: population dynamics and long-term growth depressions as indicators of changes in the Holocene hydro-regime and climate. *The Holocene* 12 (6), 695–706.
- Leuschner, H.H., Bauerochse, A., Metzler, A., 2007. Environmental change, bog history and human impact around 2900 BC in NW Germany—preliminary results from a dendroecological study of a sub-fossil pine woodland at Campemoor, Dummer Basin. *Veg. Hist. Archaeobotany* 16, 183–195.
- Linares, J.C., Senhadji, K., Herrero, A., Hodar, J.A., 2014. Growth patterns at the southern range edge of Scots pine: Disentangling the effects of drought and defoliation by the pine processionary caterpillar. *For. Ecol. Manag.* 315, 129–137.
- Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* 19, 651–663.
- Mauri, A., Davis, B.A.S., Collins, P.M., Kaplan, J.O., 2015. The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation. *Quat. Sci. Rev.* 112, 109–127.
- Mighall, T.M., Lageard, J.G.A., Chambers, F.M., Field, M.H., Mahi, P., 2004. Mineral deficiency and the presence of *Pinus sylvestris* on mires during the mid- to late Holocene: palaeoecological data from Cadogan's Bog, Mizen Peninsula, Co. Cork, southwest Ireland. *The Holocene* 14, 95–109.
- Moir, A., 2012. Development of a Neolithic pine tree-ring chronology for northern Scotland. *J. Quat. Sci.* 27, 503–508.
- Moir, A.K., Leroy, S.A.G., Brown, D., Collins, P.E.F., 2010. Dendrochronological evidence for a lower water-table on peatland around 3200–3000 BC from subfossil pine in northern Scotland. *The Holocene* 20, 931–942.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen analysis*, 2nd Edition. Blackwell Scientific Publications, Oxford.
- Niklasson, M., Drakenberg, B., 2001. A 600-year tree-ring fire history from Norra Kivills National Park, southern Sweden: implications for conservation strategies in the hemiboreal zone. *Biol. Conserv.* 101, 63–71.
- Niklasson, M., Granström, A., 2000. Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81, 1484–1499.
- Nikolaev, A., Fedorov, P.P., Desyatkin, A.R., 2009. Influence of climate and soil hydro-thermal regime on radial growth of *Larix cajanderi* and *Pinus sylvestris* in Central Yakutia, Russia. *Scandinavian J. For. Res.* 24, 217–226.
- Novák, J., Šádlo, J., Svobodová-Svitavská, H., 2012. Unusual vegetation stability in a lowland pine forest area (Doksy region, Czech Republic). *The Holocene* 22, 947–955.
- Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67, 225–249.
- Panayotov, M., Bebi, P., Tsvetanov, N., Alexandrov, N., Laranjeiro, L., Kulakowski, D., 2015. The disturbance regime of Norway spruce forests in Bulgaria. *Can. J. For. Res.* 45, 1143–1153.
- Phillips, J.D., 2013. Networks of historical contingency in Earth surface systems. *J. Geol.* 121, 1–16.
- Phillips, J.D., Šamonil, P., Pawlik, L., Trochta, J., Daněk, P., 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. *Geomorphology* 276, 27–36.
- Pilcher, J.R., Baillie, M.G.L., Schmidt, B., Becker, B., 1984. A 7272-year tree-ring chronology for western Europe. *Nature* 312, 150–152.
- Pilcher, J.R., Baillie, M.G.L., Brown, D.M., McCormac, F.G., MacSweeney, P.B., McLawrence, A.S., 1995. Dendrochronology of subfossil pine in the north of Ireland. *J. Ecol.* 83, 665–671.
- R Core Team, 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Austria, Vienna. <https://www.R-project.org/>.
- Reimer, P., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Reimer, P.J., et al., 2004. IntCal04 terrestrial radiocarbon age calibration, 0–26 cal kyr BP. *Radiocarbon* 46, 1029–1058.
- Rubino, D.L., McCarthy, B.C., 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21, 97–115.
- Šamonil, P., Doleželová, P., Vašíčková, I., Adam, D., Valtera, M., Král, K., Janík, D., Šebková, B., 2013. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *J. Veg. Sci.* 24, 1167–1184.
- Šamonil, P., Kotík, L., Vašíčková, I., 2015. Uncertainty of disturbance history detection in forest ecosystems using dendrochronology. *Dendrochronologia* 35, 51–61.
- Šamonil, P., Timková, J., Vašíčková, I., 2016. Uncertainty of the detection of disturbance spatial pattern in temperate forests. *Dendrochronologia* 37, 46–56.
- Schaffhauser, A., Payette, S., Garneau, M., Robert, E.C., 2016. Soil paludification and *Sphagnum* bog initiation: the influence of indurated podzolic soil and fire. *Boreas*. <https://doi.org/10.1111/bor.12200>.
- Schaub, M., Büntgen, U., Kaiser, K.F., Kromer, B., Talamo, S., Andersson, K.K., Rasmussen, S.O., 2008. Lateglacial environmental variability from Swiss tree rings. *Quat. Sci. Rev.* 27, 29–41.
- Schweingruber, F.H., 1988. *Tree Rings: Basics and Applications of Dendrochronology*. D. Reidel Publishing Company, Dordrecht.
- Schweingruber, F.H., 1990. *Anatomie Europäischer Hölzer*. Paul Haupt Berne und Stuttgart Publisher.
- Schweingruber, F.H., 1996. *Tree Rings and Environment: Dendroecology*. Paul Haupt, Berne.
- Schweingruber, F.H., 2007. *Wood Structure and Environment*. Springer, Berlin, GE.
- Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Broker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia* 8, 9–38.
- SCIEM, 2007. *PAST 4, Personal Analysis System for Tree Ring Research*. Available at: www.sciem.com/, Accessed date: 14 September 2018.
- Smiljančić, M., Seo, J.-W., Lääneld, A., van der Maaten-Theunissen, M., Stajić, B., Wilking, M., 2014. Peatland pines as a proxy for water table fluctuations: Disentangling tree growth, hydrology and possible human influence. *Sci. Total Environ.* 500–501, 52–63.
- Splechna, B.E., Gratzner, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest – a spatial dendroecological analysis. *J. Veg. Sci.* 16, 511–522.
- Spurk, M., Friedrich, M., Hofmann, J., Remmele, S., Frenzel, B., Leuschner, H.-H., Kromer, B., 1998. Revisions and extensions of the Hohenheim oak and pine chronologies—new evidence about the timing of the Younger Dryas/Preboreal transition. *Radiocarbon* 40, 1107–11016.
- Szewczyk, J., Szewczyk, J., Muter, E., 2011. Tree growth and disturbance dynamics in old-growth subalpine spruce forests of the Western Carpathians. *Can. J. For. Res.* 41, 938–944.

- Szwagrzyk, J., Szewczyk, J., 2001. Tree mortality and effects of release from competition in an old-growth *Fagus-Abies-Picea* stand. *J. Veg. Sci.* 12, 621–626.
- Thom, D., Rammer, W., Dirnbock, T., Muller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2017. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *J. Appl. Ecol.* 54, 28–38.
- Tollefsrud, M.M., Kissling, R., Gugerli, F., Johnsen, Ø., Skrøppa, T., Cheddadi, R., van der Knaap, W.O., Latalova, M., Terhürne-Berson, R., Litt, T., Geburek, T., Brochmann, C., Sperisen, C., 2008. Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. *Mol. Ecol.* 17, 4134–4150.
- Tolonen, K., 1986. Charred particle analysis. In: Berglund, B. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons, pp. 485–496.
- Tomlinson, P., 1985. An aid to the identification of fossil buds, bud-scales and catkin-bracts of British trees and shrubs. *Circa* 3, 45–130.
- Vašíčková, I., Šamonil, P., Ubilla, A.E.F., Kral, K., Daněk, P., Adam, D., 2016. True response of *Fagus sylvatica* L. to disturbance: a basis for empirical inference of release criteria for temperate forests. *For. Ecol. Manag.* 374, 174–185.
- Walanus, A., Nalepka, D., 2010. Calibration of Mangerud's boundaries. *Radiocarbon* 52, 1639–1644.
- Walker, M., 2005. *Quaternary Dating Methods*. Wiley, Chichester.
- Willis, K.J., van Andel, T.H., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* 23, 2369–2387.
- WRB, 2014. World Reference Base for Soil Resources, International Soil Classification system for Naming Soils and Creating Legends for Soil maps. World Soil Resources Reports no. FAO, Rome, pp. 106.
- Wright Jr., H.E., 1991. Coring tips. *J. Paleolimnol.* 6, 37–49.
- Zielonka, T., Marcher, P., 2009. The dynamics of a mountain mixed forest under wind disturbances in the Tatra Mountains, central Europe—dendrochronological reconstruction. *Can. J. For. Res.* 39, 2215–2223.
- Zielonka, T., Holeksa, J., Fleischer, P., Kapusta, P., 2010. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. *J. Veg. Sci.* 21, 31–42.